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The influence of prefire tree growth and crown condition on postfire mortality of sugar pine following prescribed fire in Sequoia National Park

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Abstract: Tree mortality is a vital component of forest management in the context of prescribed fires; however, few studies have examined the effect of prefire tree health on postfire mortality. This is especially relevant for sugar pine (*Pinus lambertiana* Douglas), a species experiencing population declines due to a suite of anthropogenic factors. Using data from an old-growth mixed-conifer forest in Sequoia National Park, we evaluated the effects of fire, tree size, prefire radial growth, and crown condition on postfire mortality. Models based only on tree size and measures of fire damage were compared with models that included tree size, fire damage, and prefire tree health (e.g., measures of prefire tree radial growth or crown condition). Immediately following the fire, the inclusion of different metrics of prefire tree health produced variable improvements over the models that included only tree size and measures of fire damage, as models that included measures of crown condition performed better than fire-only models, but models that included measures of prefire radial growth did not perform better. However, 5 years following the fire, sugar pine mortality was best predicted by models that included measures of both fire damage and prefire tree health, specifically, diameter at breast height (DBH, 1.37 m), crown scorch, 30-year mean growth, and the number of sharp declines in growth over a 30-year period. This suggests that factors that influence prefire tree health (e.g., drought, competition, pathogens, etc.) may partially determine postfire mortality, especially when accounting for delayed mortality following fire.

Key words: generalized estimating equation (GEE), tree ring analysis, forest health, *Pinus lambertiana*, Sierra Nevada.

Résumé : La mortalité des arbres est une composante essentielle de l'aménagement forestier dans le contexte des brûlages dirigés. Peu d'études ont cependant examiné l'effet de l'état de santé antérieur au feu sur la mortalité après feu. Cela est particulièrement pertinent dans le cas du pin à sucre (*Pinus lambertiana* Douglas), une espèce dont la population connaît un déclin à cause d'une série de facteurs anthropiques. À l'aide de données provenant d'une vieille forêt mélangée de conifères dans le parc national Séquoia, nous avons évalué les effets du feu, de la taille des arbres, de la croissance radiale et de l'état des cimes avant le feu sur la mortalité après feu. Des modèles fondés uniquement sur la taille des arbres et des mesures des dommages causés par le feu ont été comparés à des modèles qui incluaient la taille des arbres, les dommages causés par le feu et l'état de santé des arbres avant le feu (p. ex., des mesures de la croissance radiale et de l'état de santé de la cime des arbres avant le feu). Immédiatement après un feu, l'inclusion de différentes mesures de l'état de santé des arbres avant le feu a produit des améliorations des variables comparativement aux modèles qui incluaient seulement la taille des arbres et des mesures des dommages causés par le feu. De même, les modèles qui incluaient des mesures de l'état des cimes ont mieux performé que les modèles qui incluaient seulement les dommages causés par le feu, mais ce n'était pas le cas des modèles qui incluaient des mesures de croissance antérieures au feu. Cependant, 5 ans après un feu les modèles qui prédisaient le mieux la mortalité du pin à sucre incluaient des mesures des dommages causés par le feu et de l'état de santé des arbres avant le feu, en particulier le DHP, le roussissement de la cime, la croissance moyenne sur 30 ans et le nombre de baisses marquées de croissance sur une période de 30 ans. Cela indique que les facteurs qui influencent l'état de santé avant un feu (tels que la sécheresse, la compétition, les agents pathogènes, etc.) peuvent en partie déterminer la mortalité après feu, surtout lorsqu'on tient compte de la mortalité différée à la suite d'un feu. [Traduit par la Rédaction]

Mots-clés : équations d'estimation généralisées (EEG), analyse des cernes annuels, état de santé de la forêt, *Pinus lambertiana*, Sierra Nevada.

Introduction

Tree death is one of the most fundamental and yet complex processes controlling forest structure and dynamics (Franklin et al. 1987). To understand and predict how forests of today will look in the future, we must understand why trees die and what environmental and physical attributes or events predispose a tree to death (e.g., Waring 1987). This information is critical for improving predictions about an individual tree's future probability of mortality based on present and past conditions (Bigler and Bugmann 2004). Tree death can be a complex process that is dependent on multiple causes acting over different spatial and temporal scales. It can be sudden, caused by an event such as a flood or wildfire, or it can be a slow accumulation of factors that eventually lead to death such as competition, herbivory, disease, or

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climate change (Franklin et al. 1987). Often, however, it is an interaction between short- and long-term stressors, with both factors playing a role in controlling mortality (Manion 1991).

Tree mortality plays a critical role in determining the long-term effect of any forest fire. Tree death often defines the outcome of a forest fire, including the number and size of gaps, the availability of seed-producing trees for recovery, and the resulting forest structure and composition. Fire is both a potential threat and a critical tool for forest managers. In forests suffering from a century of fire suppression, wildfire can drastically alter the landscape, affecting forest ecosystems in profound ways (Adams 2013; Stephens et al. 2013). Yet, prescribed fire is also an essential tool for managing forest health, including reducing the risk of catastrophic wildfire, promoting species that rely on fire or fire effects for establishment, and reducing tree competition (Ryan et al. 2013).

Tree mortality after a fire occurs due to a complex interaction of weather, fuels, topography, forest condition prior to the burn, and the action of biotic agents such as bark beetles (Sieg et al. 2006). The most commonly used fire models measure fire severity in terms of postfire tree mortality, and there is substantial empirical evidence that relates fire injury, particularly crown scorch, to probability of mortality (Ryan and Reinhardt 1988; Stephens and Finney 2002; Hood et al. 2007). However, recent work has demonstrated that the severity of a fire (i.e., tree mortality) is affected not only by fire-caused damage, but also by stand conditions (Bigler et al. 2005) and forest health prior to the fire. For example, van Mantgem et al. (2003) showed that risk of mortality after fire for white fir (*Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr.) was estimated most effectively when tree growth rate was included as a measure of tree health in the predictive model. More recently, using a large regional dataset, van Mantgem et al. (2013) showed that the probability of survival after fires was associated with drought stress prior to the fire, which presumably affected tree health. In both cases, the studies tracked mortality 3–5 years after fire, incorporating delayed mortality. Accounting for delayed mortality is important, as death rates often remain elevated over background levels for up to 6 years following a fire (van Mantgem et al. 2011).

As the climate changes, the effect of prefire tree health on fire severity may become increasingly important. There is growing evidence that trees are under mounting stress as the climate warms, with mortality rates in old-growth forests increasing across western North America (van Mantgem et al. 2009; Peng et al. 2011) and the apparent incidence of drought-induced mortality events increasing worldwide (Allen et al. 2010). In addition, a warming climate is increasing the incidence (Westerling et al. 2006) and severity of wildfires across the western United States (US) (Miller and Safford 2012). In this context, our ability to quantify the effect of prefire tree health on fire severity will only continue to grow in importance.

In this study, we examined the effect of prefire tree health on postfire mortality for sugar pine (*Pinus lambertiana* Douglas), a species of management concern (van Mantgem et al. 2004; Hood 2010), by quantifying prefire tree health using tree ring patterns and visual measures of crown condition. Sugar pine is under increased stress due to several interacting factors, including the introduced pathogen white-pine blister rust (*Cronartium ribicola* A. Dietr.), mountain pine beetle (*Dendroctonus ponderosae* Hopkins), and a history of fire exclusion, which has led to increased competition, altered forest structure, and historically high fuel loads in many parts of its range (Maloney et al. 2011). Although sugar pine is a gap-adapted species that is resistant to low-severity fires due to its thick bark and open canopy, managers have become concerned that interactions among this novel combination of stressors is leading to population declines (van Mantgem et al. 2004) that may be exacerbated by the use of prescribed fire.

Quantifications of tree health, with or without fire, typically rely on short-term measures (1–5 years) of radial growth as a surrogate for tree health (e.g., van Mantgem et al. 2003). However, recent research has found that long-term measures of radial growth (up to 40 years) and those that take into account patterns in radial growth can be more effective predictors of tree mortality (Das et al. 2007). This research also demonstrated that long- versus short-term measures of radial growth provide an index of cumulative stress, allowing for more accurate predictions of mortality. Two alternative estimates of tree health besides measures of radial growth are visual estimates of crown condition (Salman and Bongberg 1942; Zarnoch et al. 2004) and live crown ratio (Dyer and Burkhart 1987). Visual health-rating protocols are commonly used to assess tree health in studies focused on measuring forest health (Innes 1993; Mangold 1998). These measures do not provide a multiyear assessment of tree health as tree ring records do but instead provide a single snapshot in time. They are much less time consuming to collect, however, and may provide an adequate estimate of tree health that can be used as an alternative to tree ring data.

We posit that long-term measures of radial growth, when combined with fire damage variables, will improve our ability to predict cumulative 5-year postfire mortality when compared with fire damage variables alone or when fire damage variables are combined with short-term measures of radial growth or crown condition. We focus on cumulative 5-year postfire mortality, as we would expect mortality immediately after a fire to primarily be a function of fire damage (i.e., trees killed outright by the fire). We use data from *P. lambertiana* with a diameter at breast height (DBH, 1.37 m) ≥ 10 cm in an area of Sequoia National Park that was recently burned to address the following questions.

(*i*) Is 5-year postfire mortality better predicted by a combination of variables that include measures of both fire damage and prefire tree health (e.g., radial growth or crown condition) compared with models based only on fire damage?
(*ii*) If so, do long-term measures of tree growth predict 5-year postfire mortality better than measures of recent growth or crown condition?

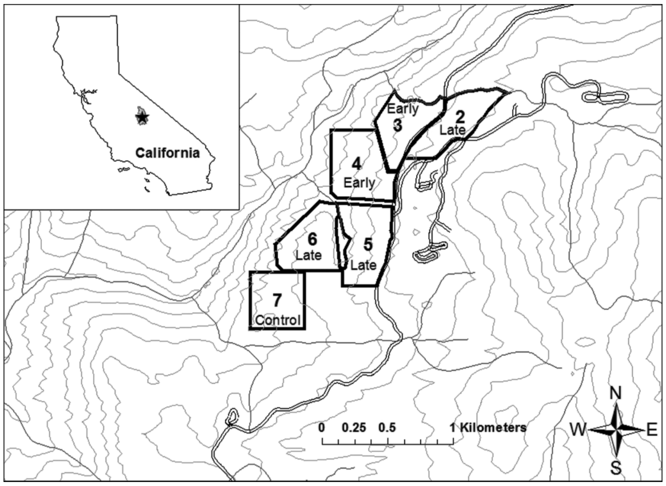
Answers to these questions will increase our understanding of the relationship between prefire tree health and postfire mortality and provide important information to managers for a species of special concern.

Methods

This study was conducted within an old-growth mixed-conifer forest in the Marble Fork drainage of Sequoia National Park, California, US (Fig. 1). The elevation ranges from 1900 m to 2150 m within the study site. Soils consist primarily of coarse loams derived from decomposed granite (Boerner et al. 2009). Mean precipitation for this area is 1200 mm·year^{-1}, with most of this falling as snow (Stephenson 1988). The most abundant overstory tree species are white fir, sugar pine, and incense cedar (*Calocedrus decurrens* (Torr.) Florin). Red fir (*Abies magnifica* A. Murray), Jeffrey pine (*Pinus jeffreyi* Balf.), and ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) also occur but at a lower abundance. The site has never been harvested and has not experienced a stand-replacing fire in >100 years (Knapp et al. 2005).

Sugar pines were sampled from within adjacent 15–20 ha prescribed burn units that were originally established as part of the national fire and fire-surrogate (FFS) study to examine the ecosystem response to silvicultural treatments that were designed to reduce fire hazard (Schwilk et al. 2009). The three treatments were as follows: early-season burn, which burned in June, late-season burn, which burned in September or October, and control, which did not burn. These treatments were randomly assigned to nine burn units. Sugar pine from five of the six early- or late-season

Fig. 1. Location of the burn units in Giant Forest, Sequoia National Park, California. Early (June 2002) and late (September–October 2001) refer to the season when the units were burned. Burn unit 7 was an unburned control. The figure was modified from Knapp et al. 2005.



burn units were sampled in this study. One additional unburned control unit was sampled to assess how postfire mortality rates in burned plots compared with background mortality rates in unburned plots. The control plots were similar in stand structure, species composition, and fuel loads to the burned plots prior to the fires (Schwilk et al. 2006). Prefire conditions including forest structure and composition were similar within all units (Schwilk et al. 2006). The types of data that were collected included information on understory and overstory vegetation (Stephens et al. 2009), fuels (Knapp et al. 2005), soils (Boerner et al. 2009), insects (Schwilk et al. 2006), and wildlife (Converse et al. 2006). Within the burn units, fifty 20 m × 50 m modified Whitaker plots (10 per burn unit) were established at permanent points along a 50 m grid system (for detailed methods of plot establishment, see Schwilk et al. (2006)). The number of plots within the burn units that contained sugar pine varied from four to nine, and the number of sugar pine within each burn unit ranged from 12 to 41.

Prior to the prescribed fires, live >1.37 m tall trees within these plots were tagged and mapped, and DBH, tree height, height to live crown, and crown condition were recorded. Live crown ratio was calculated by dividing crown length (tree height – height to live crown) by total tree height. Crown condition was measured as an ordinal variable based on a visual rating system adapted from Salman and Bongberg (1942). Each tree was assigned a rating of one if it appeared healthy and vigorous, a rating of two if there were small defects such as short needles or minor patches of dead needles or branches (flagging), a rating of three if there were substantial signs of stress such as broken tops or significant shallow crowns, or a rating of four if there were major health issues such as top dieback from blister rust or if the tree generally appeared to be near death.

Prescribed burns were conducted in two of the burn units during September or October of 2001 and in the other three burn units during June of 2002. Weather conditions were recorded hourly during the burns and were similar among burn units that occurred during the same season. Prefire fuel loads averaged 191.6 Mg·ha^{-1}, and prefire fuel moisture was similar among burn units that were ignited within the same season (Knapp et al. 2005). Fires were ignited using drip torches and were primarily strip-head fires that burned as surface fires at a low to moderate intensity. Fuel loads were reduced by 67% in the early-season burns and by 88% in the late-season burns (Knapp et al. 2005).

Following the burns, fire-caused injuries were assessed by measuring percent crown volume scorched (CrownScorch), maximum stem char height (CharHeight), and percent circumference of the base of the stem that was charred (BasalChar) for each tagged tree. Trees were then recorded as live or dead immediately (<1 year) following the fire during the summer of 2002 and then 2, 3, and 5 years following the fire. Mortality status (live or dead) was also recorded for sugar pine (n = 109) in one unburned FFS site during these same remeasures. During the summer of 2007, tree cores from all sugar pine trees with a DBH of ≥10 cm within the burned plots were collected (96 dead and 69 live). Only live trees with a DBH of ≥10 cm at the time of the burn were used in this study to ensure that long-term growth records (at least 30 years) were available and because it was assumed that most trees with a DBH of <10 cm would not survive the fire.

One core was collected per tree at breast height. In a few cases, a second core was collected if there was question about the integrity of the first core. If the first core proved to be usable, the second core was not read. Cores were then mounted and sanded to allow for an accurate measure of ring width. Rings were measured using a dissecting microscope and a sliding-stage micrometer to 0.01 mm accuracy. Many of the trees that died following the fire had significant rot, as they had been dead for several years, resulting in only 105 trees (55 dead and 50 live) producing readable cores of at least 30 years in length. Seventeen of the live tree cores were excluded because of breaks in the cores or an insufficient number of rings, and another two of the live tree cores were excluded because of missing data such as missing DBH or measures of fire damage.

As part of our error-checking procedures, we cross-dated cores to help identify false or missing rings. A master chronology was developed from 21 cores with the greatest number of rings and was used to check the cores for errors, including missing or false rings, using COFECHA (Grissino-Mayer 2001). Any cores with missing or extra rings, as indicated by COFECHA, were visually inspected to confirm the errors, using known marker years as a guide. No changes were made to a measurement series unless the error was visually identified on the core itself (e.g., finding partial rings that were missed or false rings that were counted). Cores that cross-dated poorly (<0.1 correlation) were remeasured to validate the original measurements. The overall series intercorrelation among the 105 cores with the master chronology was 0.322 and had a mean sensitivity (a measure of interannual variability) of 0.213. Crossdating was only used as a method of error checking. No cores were excluded due to an inability to cross-date.

Data analysis

The overall goal of the analysis was to test whether models that included measures of prefire radial growth or tree crown condition in addition to size and fire damage variables predicted immediate (<1 year) and 5-year postfire mortality better than models based on tree size and fire damage variables alone. Logistic regression models were used to model probability of postfire tree mortality (Hosmer and Lemeshow 2000). Given the nested structure of the data (i.e., with trees nested within plots), we used generalized estimating equation (GEE) models to account for the potential correlation of trees within plots (Hardin and Hilbe 2012). A GEE model is a common approach used with correlated data that estimates model parameters through an iterative process of solving a set of equations based on a quasi-likelihood distribution. It is predicated on a marginal (population mean) interpretation of model parameters compared with a conditional (subject-specific) interpretation of model parameters employed by generalized linear mixed models (GLMM), another common approach used to analyze non-normal hierarchical data (Fieberg et al. 2009). The GEE model approach has been shown to be preferable to GLMM when the goal is to compare population-level expected responses (Alencar et al. 2012), as is the case in this study (see Supplementary

Fig. S1 for a comparison between GEE and GLMM models[1]). Because of the binary nature of our response variable (live or dead), the models used a logit link function and assumed a binomial distribution. The logit link function is used to convert the response variable (probability of mortality) into a continuous variable that is linear with respect to the explanatory variables (Hosmer and Lemeshow 2000).

Several variables must be specified when fitting a GEE model, including a regression model of the mean and variance and a model of the correlation structure of the data. Several working correlation structures are possible, including independent, exchangeable, and autoregressive structures, as well as other structures (Hardin and Hilbe 2012). One appealing property of GEE models is that they are robust to misspecifications of the correlation structure (Ziegler and Vens 2010). We used an exchangeable correlation structure in the regression analyses, as we felt that this structure was most appropriate for our data and has been used in similar studies of tree mortality (Thies et al. 2006). This sets the correlation between any two responses in a sample unit as equal and treats individuals from different sample units as independent (Liang and Zeger 1986).

Model fit relative to other tested models was assessed using a quasi-information criterion (QIC; Pan 2001). The QIC is similar to the more well-known Akaike's information criterion (AIC) but is based on quasi-likelihood estimation instead of maximum likelihood estimation (Pan 2001). QIC was also used to evaluate the selection of an exchangeable correlation structure compared with an independent correlation structure to examine the effect of the nested structure of our data on parameter estimates. We defined a meaningful change in model fit as a difference in QIC between models of ≥2, a commonly used cutoff with AIC (Burnham and Anderson 2002).

Models based on tree size, fire damage variables, tree health variables, and all variables combined were compared to assess whether the inclusion of measures of prefire tree health would substantially improve the predictive power of sugar pine mortality immediately following the fire and 5 years after the fire. Model selection was carried out over several steps. First, the degree of correlation between the fire damage variables was assessed, and no pair of fire damage parameters displayed a correlation of >0.6. Next, a full model that included the effect of DBH, fire season, and measures of fire damage (CrownScorch, CharHeight, and BasalChar) was evaluated for both immediate postfire mortality and 5-year postfire mortality. Then, backwards stepwise elimination was used to remove variables with low explanatory power from the model. Lastly, the variable with the lowest Wald statistic was removed until all remaining parameters in the model were significant (Hosmer and Lemeshow 2000).

Once the final model was selected for predicting immediate and 5-year postfire mortality based only on measures of tree size and fire damage, several different combinations of radial tree growth or crown condition variables were added to evaluate whether the inclusion of these parameters significantly improved model performance. There were seven different measures of radial growth in all, including annual growth immediately preceding the fire, mean growth over 5 and 30 years preceding the fire, growth trend (defined as the linear rate of increase or decrease in growth over 5 and 30 years), and number of sharp declines in growth over 5 and 30 years. Sharp declines were defined as any annual decline in growth ≥ 50% relative to the previous year. Time periods of 5 and 30 years preceding the fire were selected because past research has found growth over a 5-year period to predict mortality probabilities (van Mantgem et al. 2003) and 30 years was the longest time period measured from the tree cores that could be assessed without having to further reduce sample size.

Each of the seven measures of tree radial growth was calculated using radial increment. Other studies have also calculated growth based on basal area increment or relative basal area increment (current annual basal area increment divided by initial basal area). Currently, there is no consensus in the literature as to which metric of growth is best; some have preferred radial increment (Das et al. 2007), others have preferred basal area increment (Pedersen 1998; Bigler and Bugmann 2004), and still others have preferred relative basal area increment (Disalvo and Hart 2002; Karlsson et al. 2006). Each has a different relationship with tree size and, therefore, produces slightly different results. The analysis was also conducted using growth measured as basal area and as relative basal area, but no one measure preformed consistently better than the others. We, therefore, chose to use radial increment, as it is easy to interpret and has been used in previous studies that evaluated the effects of long-term growth on the probability of mortality for sugar pine (Das et al. 2007).

Each growth index (mean growth, growth trend, and number of sharp declines) and all combinations within each time frame (5 or 30 years) were tested in combination with the selected fire damage variables, producing a total of 14 fire + growth models. The annual increment from the year immediately preceding the fire was also tested, so the total number of fire + growth models that were evaluated was 15. Models based on two measures of crown condition (visual crown health rating and live crown ratio) were also tested both separately and in combination with the fire damage variables for a total of three fire + crown condition models. Through the examination of contrast tests of models that included levels of the ordinal variable crown health rating, we found that the logits followed a linear pattern and could be treated as a numeric factor instead of an ordered factor in the models. This improved the model fit and simplified the interpretation of the model coefficients. In all, a total of 22 models (4 fire-only models, 15 fire + growth models, and 3 fire + crown condition models) were evaluated for both immediate and 5-year postfire mortalities (see Supplementary Table S1 for a full summary of models that were tested).

For each set of models (fire only, fire + growth, fire + crown condition), the best model or models were selected based on QIC scores. A change in QIC of ≥2 was used as an indicator of a significant difference between model fits. Equivalent models (QIC within two units of the best ranked model) are presented as alternative models with similar performance. Model discrimination between dead and live trees was assessed using the receiver operating characteristic (ROC). A higher area under the ROC curve (AUC) value indicates that a higher proportion of trees was correctly classified as live or dead by the model (Hosmer and Lemeshow 2000). The percentage of trees correctly classified by each model was also reported based on an optimal cut point determined by the data. The optimal cut point is the predicted survival probability that maximizes model sensitivity and specificity. Model calibration was assessed using linear logistic calibration plots from the val.prob function in the rms R package (Harrell 2014), and we found no bias in the predictions. All analyses were conducted in R 3.1.1 (R Core Team 2014) and relied on several packages, including geepack (Højsgaard et al. 2006), lme4 (Bates et al. 2014), and pROC (Robin et al. 2011).

Results

Of the 105 sugar pine, 55 (52.4%) were dead 5 years following the fire, with 25 dying immediately following the fire (Table 1). The annual mortality rate peaked at 23.8% immediately after the fire

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2014-0449.

Table 1. Summary statistics for 105 sugar pine recorded immediately after the fire and 5 years after the fire in Sequoia National Park.

	Immediate after the fire		5 years after the fire	
	Live	Dead	Live	Dead
No. of trees	80	25	50	55
DBH (cm)	45.1 (3.8)	19.0 (1.8)	50.7 (4.2)	28.1 (4.1)
Live crown ratio	0.76 (0.02)	0.77 (0.04)	0.76 (0.02)	0.77 (0.03)
Crown health rating	2.0 (0.1)	3.2 (0.2)	1.8 (0.1)	2.8 (0.2)
Prefire growth rate (mm·year⁻¹)				
5 years	1.75 (0.13)	0.94 (0.14)	2.11 (0.18)	1.06 (0.10)
30 years	1.79 (0.11)	1.09 (0.12)	2.12 (0.14)	1.16 (0.09)
Prefire growth trend (mm·year⁻¹)				
5 years	–0.07 (0.01)	–0.09 (0.02)	–0.08 (0.02)	–0.06 (0.02)
30 years	0.05 (0.39)	–1.05 (0.39)	0.43 (0.50)	–0.80 (0.38)
No. of sharp declines				
5 years	0.16 (0.05)	0.32 (0.10)	0.12 (0.05)	0.27 (0.06)
30 years	0.60 (0.12)	1.36 (0.26)	0.26 (0.07)	1.25 (0.19)
CrownScorch (%)	23.5 (3.5)	88.2 (6.5)	18.6 (3.7)	57.4 (6.1)
CharHeight (m)	2.7 (0.5)	2.4 (0.4)	3.0 (0.7)	2.3 (0.4)

Note: Values in parentheses indicate standard errors. DBH, diameter at breast height (1.37 m); CrownScorch, crown volume scorched; CharHeight, maximum stem char height.

and declined steadily over the course of the study to the point where no new mortality occurred between 2006 and 2007 (Fig. 2). The annual mortality rate 4 years and 5 years following the fire was similar to the background mortality rates of sugar pine within the adjacent unburned control plot. Trees were split evenly between units ignited in the spring and in the fall, with 53 trees in the spring burns and 52 trees in the fall burns. Mortality rates were similar between burn seasons (Table 1), and this term was never a significant predictor of mortality in any of the tested models. The mean prefire DBH of trees that survived 5 years after the fire was 50.7 cm compared with 28.1 cm for trees that were dead (Table 1). CrownScorch displayed a bimodal distribution, with the crown of many trees either being scorched completely or not at all. Median CrownScorch was 5% for live trees 5 years after the fire compared with 90% for dead trees. CharHeight was strongly skewed to the right, with most trees receiving either no or very little (<2 m) charring, with a few trees that were charred >15 m up the stem (range = 0–19 m). The median CharHeight of live trees was 95 cm compared with 145 cm for dead trees. BasalChar also displayed a bimodal distribution and was significantly lower in live trees than in dead trees, with median values of 80% and 100%, respectively.

Percent live crown ratio was similar between live and dead trees, with median values of 0.78 and 0.80, respectively (Table 1). The prefire crown condition rating of live trees averaged 1.8 compared with 2.8 for dead trees 5 years after the fire (Table 1), with most trees with a poor crown condition rating (i.e., 4) prior to the burn dying within 5 years after the fire (Fig. 3).

Models of immediate postfire mortality

The best models to predict immediate postfire mortality included DBH, CrownScorch, BasalChar, and measures of crown condition (Table 2). These models showed an improvement in model performance relative to the fire-only models. The two best fire + crown condition models included crown condition rating and crown condition rating + live crown ratio and had QIC scores of 53.78 and 51.89, respectively. The model that included both measures of crown condition had an AUC of 0.972 and classified 95% of all trees correctly (96% of live trees were classified correctly and 95% of dead trees were classified correctly) using an optimal cut point of 0.51. Tree size had a significant negative relationship with the probability of mortality, and larger trees were less likely to die immediately after the fire (Table 3). CrownScorch was also a significant predictor of immediate postfire mortality and had a positive relationship with immediate postfire mortality (Wald test, $p < 0.001$). BasalChar, however, displayed the inverse relationship than would be expected, as its coefficient indicated that after accounting for DBH and CrownScorch, trees with more BasalChar were less likely to die immediately after the fire (Table 3). In the model that included only tree size and measures of fire damage, BasalChar was not a significant predictor of mortality (Wald test, $p = 0.07$), although its inclusion did result in a slight improvement in the QIC (Table 2). The coefficient estimate of the crown condition rating was positive, indicating that trees with less healthy crowns had a higher probability of mortality immediately after the fire (Wald test, $p = 0.02$). The coefficient for live crown ratio was negative, which would indicate that trees with larger live crown ratios were more likely to die immediately after the fire, but this parameter was not significant (Wald test, $p = 0.20$).

Models to predict immediate postfire mortality based on measures of tree size and fire damage alone also fit the data well. The best predictors of mortality immediately after the fire when only fire damage variables and tree size were considered were DBH, CrownScorch, and BasalChar (Table 2). The logistic regression model using these explanatory variables had an AUC of 0.963, indicating high discrimination in the classification of live and dead trees. This model classified 88% of all trees correctly (67% of

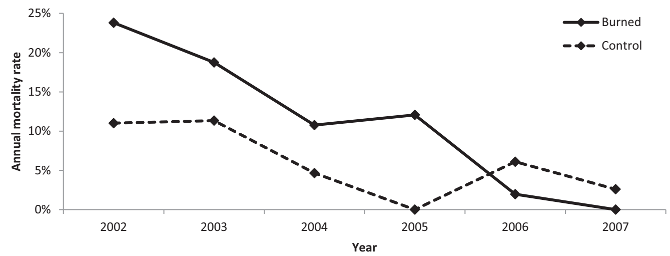


Fig. 2. Annual postfire mortality rate of sugar pine in the study area. By 2007, 55 of the 105 trees in the burned plots had died (mean annual mortality = 9%), and 34 of the 109 trees in the control plot had died (mean annual mortality = 5%).

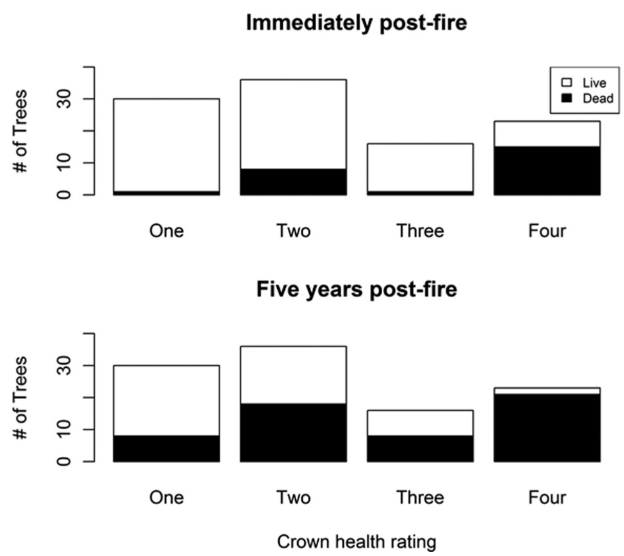


Fig. 3. Sugar pine mortality by crown health rating immediately and 5 years after the fire in Sequoia National Park, California. Each tree was assigned an ordinal rating of one to four, with one indicating that the crown appeared healthy and vigorous and four indicating major signs of stress and that the tree generally appeared near death.

Table 2. Best generalized estimating equation (GEE) models to predict immediate postfire mortality.

Model type	Parameters	QIC	ΔQIC
Fire + crown condition	DBH+CrownScorch+BasalChar+CrownCond+LiveCrown	51.89	−4.11
Fire + crown condition	DBH+CrownScorch+BasalChar+CrownCond	53.78	−2.22
Fire + growth (last year)	DBH+CrowScorch+BasalChar+LastYearDiam	55.14	−0.86
Fire	DBH+CrownScorch+BasalChar	56.00	0.00
Fire	DBH+CrownScorch	56.61	0.61
Fire + growth (5 years)	DBH+CrownScorch+BasalChar+Decline5	57.88	1.88
Fire + growth (30 years)	DBH+CrownScorch+BasalChar+Trend30	58.38	2.38
Fire + growth (5 years)	DBH+CrownScorch+BasalChar+Trend5	58.84	2.84
Fire + growth (5 years)	DBH+CrownScorch+BasalChar+Ave5	59.35	3.35

Note: Model type indicates the explanatory variables used in the models. All models included diameter at breast height (DBH, 1.3 m) and measures of fire damage. Models that also included measures of radial growth are classified as fire + growth models, and models that included measures of crown condition are classified as fire + crown condition models. QIC, quasi information criterion; CrownScorch, crown volume scorched; BasalChar, percent circumference of the base of the stem that was charred; CrownCond, a visual rating of crown health; LiveCrown, live crown ratio; LastYearDiam, annual radial growth 1 year prior to the fire; Decline5, number of sharp declines in growth over 5 years; Trend30 and Trend5, growth trend over 30 and 5 years, respectively; Ave5, average radial growth over 5 years. DQIC values are relative to the best fire-only model.

Table 3. Coefficient estimates and standard errors (SE) for best fire-only model, fire + growth model, and fire + health model to predict immediate postfire mortality.

	Fire only			Fire + growth			Fire + crown condition		
Immediate postfire mortality	Estimate	SE	*p* value	Estimate	SE	*p* value	Estimate	SE	*p* value
Intercept	0.748	1.187	0.529	2.008	1.286	0.119	1.011	2.101	0.631
DBH	−0.112	0.038	0.003	−0.107	0.041	0.012	−0.133	0.060	0.026
CrownScorch	0.073	0.024	0.003	0.075	0.021	<0.001	0.078	0.013	<0.001
BasalChar	−0.043	0.024	0.070	−0.050	0.021	0.016	−0.045	0.014	<0.001
LastYearDiam	—	—	—	−1.130	0.537	0.036	—	—	—
LiveCrown	—	—	—	—	—	—	−2.681	2.108	0.203
CrownCond	—	—	—	—	—	—	0.986	0.423	0.020

Note: All models included diameter at breast height (DBH, 1.37 m) and two measures of fire damage: percent crown volume scorched (CrownScorch) and percent circumference of the base that was charred (BasalChar). The fire + growth model also included annual radial growth 1 year prior to the fire (LastYearDiam), and the fire + crown condition model also included live crown ratio (LiveCrown) and visual crown condition rating (CrownCond).

live trees were classified correctly and 99% of dead trees were classified correctly), using an optimal cut point of 0.81.

Models of immediate postfire mortality that included measures of prefire radial growth in addition to measures of fire damage displayed no improvement in model performance compared with models based only on measures of fire damage and tree size or models that included fire damage, tree size, and crown health parameters (Table 2). The only measure of radial growth that improved model fit compared with the fire-only and tree size only models was annual radial growth 1 year before the fire; however, this model did not perform substantially better than the fire-only model (ΔQIC = −0.86).

Models of 5-year postfire mortality

When delayed mortality was accounted for, models that included measures of fire damage and tree size, as well as measures of radial growth or crown condition, performed substantially better than models that included only measures of fire damage and tree size. Models that included long-term measures of radial growth outperformed models that included immediate prefire growth or 5-year prefire growth (Table 4). The improvement in fit is most evident when CrownScorch is high, as the fire + growth model has a narrower 95% confidence interval compared with the fire-only model (Fig. 4). The model that best predicted 5-year postfire mortality included 30-year mean growth and the number of rapid declines within the 30-year period (Table 5). This model had an AUC of 0.916, classifying 87% of all trees correctly (96% of live trees and 78% of dead trees) using an optimal cut point of 0.35. Of the trees that did not die immediately after the fire, 84% were classified correctly. The coefficient estimate of the mean 30-year growth was negative, indicating that trees with increasing growth rates were less likely to die after the fire, whereas the coefficient for the number of sharp declines was positive, indicating that trees with more sharp declines were more likely to die after the fire (Table 5). Regardless of what measure of radial growth was used, almost all models that contained some measure of prefire growth and fire damage performed significantly better at predicting 5-year postfire mortality than models with only fire damage and tree size, with 11 of the 15 fire + growth models exhibiting substantially lower QIC scores than the best fire damage and tree size only model.

Including visual crown condition rating or live crown ratio did improve model fit compared with the fire damage and tree size only model, though not nearly as much as the models that included measures of radial growth (Table 4). The best fire + crown condition model included crown condition rating and had a QIC of 98.44, a substantial improvement (ΔQIC = −3.69) over the best fire-only model. The model had an AUC of 0.879 and predicted 85% of all trees correctly (88% of live trees and 81% of dead trees), using an optimal cut point of 0.44. The coefficient estimate of crown condition rating was positive (Table 5), indicating that trees with healthier visual crown characteristics (lower rating) had a lower probability of mortality 5 years after fire. The inclusion of live crown ratio did not improve model fit.

The best model based only on measures of fire damage and tree size included DBH and CrownScorch as the explanatory variables and had a QIC of 102.16. Increasing tree size had a negative effect

Table 4. Best generalized estimating equation (GEE) models to predict 5-year postfire mortality.

Model type	Parameters	QIC	ΔQIC
Fire + growth (30 years)	DBH+CrownScorch+Ave30+Decline30	83.77	–18.36
Fire + growth (5 years)	DBH+CrownScorch+Ave5	92.41	–9.72
Fire + growth (last year)	DBH+CrowScorch+LastYearDiam	95.00	–7.13
Fire + crown condition	DBH+CrownScorch+CrownCond	98.44	–3.69
Fire	DBH+CrownScorch	102.13	0

Note: Model type indicates the explanatory variables used in the models. All models included diameter at breast height (DBH, 1.37 m) and percent crown volume scorched (CrownScorch). Models that also included measures of radial growth (Ave30 and Ave5 are the mean growth rate 30 and 5 years before the fire, respectively, and Decline30 is the number of sharp declines over the 30 years before the fire) are classified as fire + growth models. Models that included measures of crown condition (CrownCond is a visual rating of crown health) are classified as fire + crown condition models. QIC, quasi information criterion. ΔQIC values are relative to the best fire-only model.

Fig. 4. Comparison of fire effects only and fire + growth generalized estimating equation (GEE) models for predicting 5-year postfire mortality. Explanatory variables in the fire effects only model were DBH and percent crown volume scorched (crown scorch). Explanatory variables in the fire + growth GEE model were DBH, crown scorch, mean 30-year growth rate, and the number of sharp declines over 30 years. Mean 30-year growth rate was held constant at 1.63 mm·year^{-1} (the mean value of all trees), and the number of sharp declines was held constant at 0. DBH was held constant at 37.29 (the mean value of all trees) for both models. 95 Conf. int., 95% confidence interval.

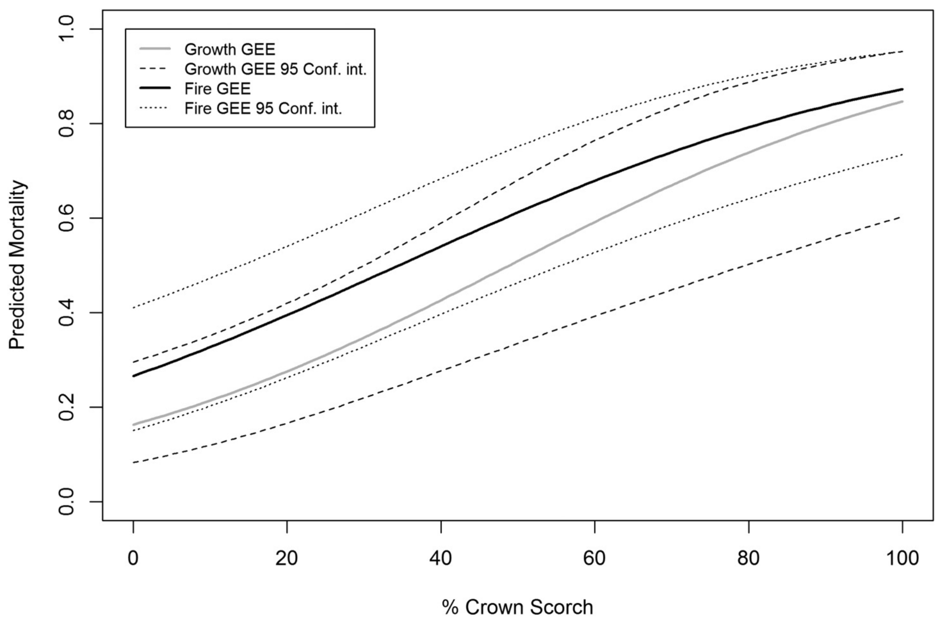


Table 5. Coefficient estimates and standard errors (SE) for best fire-only model, fire + growth model, and fire + crown condition model to predict 5-year postfire mortality.

	Fire only			Fire + growth			Fire + crown condition		
	Estimate	SE	*p* value	Estimate	SE	*p* value	Estimate	SE	*p* value
Intercept	0.754	0.527	0.152	1.096	0.677	0.105	–0.965	0.745	0.195
DBH	–0.047	0.016	0.004	–0.037	0.014	0.006	–0.037	0.015	0.019
CrownScorch	0.029	0.006	<0.001	0.033	0.008	<0.001	0.029	0.007	<0.001
Ave30	—	—	—	–0.820	0.342	0.017	—	—	—
Decline30	—	—	—	0.835	0.245	<0.001	—	—	—
CrownCond	—	—	—	—	—	—	0.610	0.228	0.008

Note: All models included diameter at breast height (DBH, 1.37 m) and percent crown volume scorched (CrownScorch). The best fire + growth model also included mean radial growth over 30 years prior to the fire (Ave30) and the number of sharp declines in growth over the same time period (Decline30). The best fire + crown condition model also included a visual rating of crown health (CrownCond).

on the postfire probability of mortality, whereas increasing CrownScorch had a positive effect on the postfire probability of mortality (Table 5). The fire-only model had an AUC of 0.866 and classified 83% of all trees correctly (80% of live trees and 85% of dead trees) using an optimal cut point of 0.53. Of the trees that did not die immediately after fire, only 77% were classified correctly.

Discussion

Models that included long-term measures of radial growth were substantially better at predicting 5-year postfire mortality than models with tree size and fire damage variables alone or models that included only short-term measures of tree growth and measures of fire damage. This supports the idea that prefire tree health is important for predicting postfire mortality and confirms the effectiveness of using tree ring patterns for estimating the probability of mortality following prescribed fire for sugar pine. This finding aligns with the more general observation that trees that are exposed to chronic stressors and grow more slowly are more likely to die when confronted with additional acute stressors (Manion 1991; Franklin et al. 1987). This concept has been supported by others who have found that trees experiencing a long-term stress such as competition are more susceptible to short-term stresses such as drought (Linares et al. 2010). In addition, the effect of previous stress on tree health appears to be cumulative, as past events, even if in the distant past, can make trees more susceptible to mortality (Pedersen 1998; Das et al. 2007). Das et al. (2007) found that combinations of several measures of radial growth, including mean long-term growth rate, growth trend measured as the slope of growth over time, and the number of sharp declines in growth rate over the past 40 years could substantially improve predictive models of tree mortality in unburned stands. Our results extend these findings to burned stands, as measures of fire damage combined with long-term mean growth and the number of abrupt declines in growth substantially improved estimates of mortality risk compared with models based only on measures of recent growth in sugar pine.

The superiority of the models that included measures of prefire tree growth or crown condition for predicting 5-year postfire mortality appears largely to be a function of delayed mortality, as fire + growth models were able to correctly classify the 5-year postfire status of trees that survived the first year after a fire more accurately than models that did not include prefire measures of radial growth or crown condition. When the best fire + growth model and the best fire-only model were reparameterized using only trees that were still alive immediately after the fire (n = 80), the fire + growth model performed substantially better (QIC = 78.6 versus 92.9). Immediate mortality, however, was best described by fire + crown condition models, although fire-only models still performed quite well, indicating that prefire tree growth only becomes important for trees that survive the initial damage from the fire.

The inclusion of delayed mortality is clearly critical for understanding the cumulative effects of a fire, and although often ignored, this additional mortality can alter model predictions and accuracy substantially. One way to account for delayed mortality is to incorporate measures of prefire growth into the predictive model, as this seems to be a driving factor in discriminating between trees that will eventually die and trees that will survive.

Of course, the use of tree ring data to predict mortality comes at a cost. It poses a practical obstacle in that acquiring and processing tree ring samples can be expensive and time consuming. In contrast, visual estimates of crown condition such as live crown ratio or a crown condition rating and even short-term growth rate require a substantially smaller investment of resources. Other substitutes for tree ring data besides crown condition may include relative drought stress (van Mantgem et al. 2013) or repeated measures of DBH, which can be used to calculate mean prefire growth rate (van Mantgem et al. 2003). These measures will likely be inferior to the use of tree ring patterns for predicting cumulative postfire mortality, but the inclusion of short-term measures of growth or prefire crown condition still offer some improvement over models that rely on fire damage variables alone.

Ultimately, the needs of a given manager will determine the balance of cost versus benefit for a particular project. For example, in the case of sugar pine, managers may deem the extra effort for collecting tree rings to be justified. As previously noted, sugar pine may be at higher risk of mortality following fire due to multiple factors such as blister rust, increased fuel loads, and changes in climate (Tomback and Achuff 2010). Managers at Sequoia and Kings Canyon national parks, for example, have already shown an interest in protecting individual sugar pines during prescribed fires (Nesmith et al. 2010), and the extra effort of collecting tree rings to identify the most vulnerable trees might be justified in some cases.

More broadly, this study adds to a growing body of research suggesting that understanding the long-term impact of fire, particularly in the context of climate change, cannot be fully quantified without considering tree health prior to the fire (Allen et al. 2010; van Mantgem et al. 2013). Whether mangers are able to collect tree rings or rely on other metrics, the importance of incorporating the tree and stand conditions when trying to understand the potential effects of a burn (planned or otherwise) is becoming increasingly clear.

Although we have only examined one species in this study, it seems quite likely that our findings will apply generally to conifer species in the Sierra Nevada or in other areas of the western US. Other questions remain unanswered, including whether accounting for other environmental trends such as climate would further improve models and whether models can be improved by creating separate predictive models for trees that die immediately after fire and for those for which mortality is delayed for one or more years.

Prescribed fire has become one of the main silvicultural tools used for management and restoration of sugar pine in the Sierra Nevada (North et al. 2007). A better understanding of long-term postfire mortality is critically important for achieving management objectives for sugar pine given that local population declines are expected to continue (van Mantgem et al. 2004). This research implies that managers should expect higher mortality from prescribed fire after periods of drought or other stress, even when current fuel moisture levels are normal, and that increased mortality will be driven by delayed mortality, as weakened trees are less likely to recover from the effects of the fire.

Conclusions

Predicting mortality following a fire is an important goal for forest managers. Models based on tree size and various measures of fire damage are most commonly used to accomplish this. Although special attention is often paid to fuel loads and fire weather during prescribed fires to control postfire mortality rates, the potential effects of prefire tree health are rarely considered. However, this study has shown that factors that influence prefire tree health can ultimately influence postfire survivorship and can lead to an increase in fire severity without changing fire intensity. Therefore, incorporating measures of prefire tree health into models of postfire mortality, especially measures of long-term radial growth, can substantially improve cumulative postfire mortality predictions. This study also found that long-term measures of growth produced substantial improvements in model performance compared with short-term measures and should be preferred when long-term growth data are available.

As the climate continues to change, with forests experiencing increasing stress and perhaps requiring increasing management intervention, our need to accurately predict the effect of fire on the landscape continues to grow. This work supports the notion that we can only understand fire in the biological context in which it occurs, with the condition of the forest likely playing an important role.

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References

Adams, M.A. 2013. Mega-fires, tipping points and ecosystem services: managing forests and woodlands in an uncertain future. For. Ecol. Manage. **294**: 250–261. doi:10.1016/j.foreco.2012.11.039.

Alencar, A., Singer, J., and Rocha, F. 2012. Competing regression models for longitudinal data. Biom. J. **54**(2): 214–229. doi:10.1002/bimj.201100056.

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., and Cobb, N. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manage. **259**: 660–684. doi:10.1016/j.foreco.2009.09.001.

Bates, D., Maechler, M., Bolker, B., and Walker, S. 2014. lme4: linear mixed-effects models using Eigen and S4. R package version 1.1–7. Available from http://CRAN.R-project.org/package=lme4.

Bigler, C., and Bugmann, H. 2004. Predicting the time of tree death using dendrochronological data. Ecol. Appl. **14**(3): 902–914. doi:10.1890/03-5011.

Bigler, C., Kulakowski, D., and Velben, T.T. 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain subalpine forests. Ecology, **86**(11): 3018–3029. doi:10.1890/05-0011.

Boerner, R.E.J., Huang, J., and Hart, S.C. 2009. Impacts of fire and fire surrogate treatments on forest soil properties: a meta-analytical approach. Ecol. Appl. **19**(2): 338–358. doi:10.1890/07-1767.1.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer, New York.

Converse, S.J., White, G.C., Farris, K.L., and Zack, S. 2006. Small mammals and forest and fuel reduction: national-scale responses to fire and fire surrogates. Ecol. Appl. **16**(5): 1717–1729. doi:10.1890/1051-0761(2006)016[1717:SMAFFR]2.0.CO;2.

Das, A., Battles, J.J., Stephenson, N.L., and van Mantgem, P.J. 2007. The relationship between tree growth patterns and likelihood of mortality: a study of two tree species in the Sierra Nevada. Can. J. For. Res. **37**(3): 580–597. doi:10.1139/X06-262.

Disalvo, A.C., and Hart, S.C. 2002. Climatic and stream-flow controls on tree growth in a western montane riparian forest. Environ. Manage. **30**(5): 678–691. doi:10.1007/s00267-002-2719-2.

Dyer, M., and Burkhart, H. 1987. Compatible crown ratio and crown height models. Can. J. For. Res. **17**(6): 572–574. doi:10.1139/x87-096.

Fieberg, J., Rieger, R.H., Zicus, M.C., and Schildcrout, J.S. 2009. Regression modelling of correlated data in ecology: subject-specific and population averaged response patterns. J. Appl. Ecol. **46**: 1018–1025. doi:10.1111/j.1365-2664.2009.01692.x.

Franklin, J.F., Shugart, H.H., and Harmon, M.E. 1987. Tree death as an ecological process. BioScience, **37**(8): 550–556. doi:10.2307/1310665.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res. **57**(2): 205–221.

Hardin, J.W., and Hilbe, J.M. 2012. Generalized estimating equations. 2nd edition. Chapman & Hall, Boca Raton, Florida.

Harrell, F.E., Jr. 2014. Package "rms". Vanderbilt University, Nashville, Tennessee, USA.

Højsgaard, S., Halekoh, U., and Yan, J. 2006. The R package geepack for generalized estimating equations. J. Stat. Softw. **15**(2): 1–11.

Hood, S.M. 2010. Mitigating old tree mortality in long-unburned, fire-dependent forests: a synthesis. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, Gen. Tech. Rep. RMRS-GTR-238.

Hood, S.M., McHugh, C.W., Ryan, K.C., Reinhardt, E., and Smith, S.L. 2007. Evaluation of a post-fire tree mortality model for western U.S.A. conifers. Int. J. Wildland Fire, **16**: 679–689. doi:10.1071/WF06122.

Hosmer, D.W., and Lemeshow, S. 2000. Applied logistic regression. John Wiley and Sons, New York.

Innes, J.L. 1993. Forest health: its assessment and status. CAB International, Wallingford, Oxon, UK.

Karlsson, P.E., Örlander, G., Langvall, O., Uddling, J., Hjorth, U., Wiklander, K., Areskoug, B., and Grennfelt, P. 2006. Negative impact of ozone on the stem basal area increment of mature Norway spruce in south Sweden. For. Ecol. Manage. **232**: 146–151. doi:10.1016/j.foreco.2006.05.059.

Knapp, E.E., Keeley, J.E., Ballenger, E.A., and Brennan, T.J. 2005. Fuel reduction and coarse woody debris dynamics with early season and late season prescribed fire in a Sierra Nevada mixed conifer forest. For. Ecol. Manage. **208**: 383–397. doi:10.1016/j.foreco.2005.01.016.

Liang, K.Y., and Zeger, S.L. 1986. Longitudinal data analysis using generalized linear models. Biometrika, **73**(1): 13–22. doi:10.1093/biomet/73.1.13.

Linares, J.C., Camarero, J.J., and Carreira, J.A. 2010. Competition modulates the adaptation capacity of forests to climatic stress: insights from recent growth decline and death in relict stands of the Mediterranean fir *Abies pinsapo*. J. Ecol. **98**: 592–603. doi:10.1111/j.1365-2745.2010.01645.x.

Maloney, P.E., Vogler, D.R., Eckert, A.J., Jensen, C.E., and Neale, D.B. 2011. Population biology of sugar pine (*Pinus lambertiana* Dougl.) with reference to historical disturbances in the Lake Tahoe Basin: implications for restoration. For. Ecol. Manage. **262**: 770–779. doi:10.1016/j.foreco.2011.05.011.

Mangold, R.D. 1998. Overview of the forest health monitoring program. *In* Integrated tools for natural resources inventories in the 21st century. *Edited by* H. Hansen and T. Burk. USDA Forest Service, Boise, Idaho, Gen. Tech. Rep. NRCS-212. pp. 129–140.

Manion, P.D. 1991. Tree disease concepts. 2nd edition. Prentice Hall, Englewood Cliffs, New Jersey.

Miller, J.D., and Safford, H.D. 2012. Trends in wildfire severity: 1984 to 2010 in the Sierra Nevada, Modoc Plateau, and southern Cascades, California, U.S.A. Fire Ecology, **8**(3): 41–57. doi:10.4996/fireecology.0803041.

Nesmith, J.C.B., O'Hara, K.L., van Mantgem, P.J., and de Valpine, P. 2010. The effects of raking on sugar pine mortality following prescribed fire in Sequoia and Kings Canyon National Parks, Califorina, U.S.A. Fire Ecology, **6**(3): 97–116. doi:10.4996/fireecology.0603097.

North, M., Innes, J., and Zald, H. 2007. Comparison of thinning and prescribed fire restoration treatments to Sierran mixed-conifer historic conditions. Can. J. For. Res. **37**(2): 331–342. doi:10.1139/X06-236.

Pan, W. 2001. Akaike's information criterion in generalized estimating equations. Biometrics, **57**(1): 120–125. doi:10.1111/j.0006-341X.2001.00120.x.

Pedersen, B.S. 1998. Modeling tree mortality in response to short- and long-term environmental stresses. Ecol. Model. **105**: 347–351. doi:10.1016/S0304-3800(97)00162-2.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X., and Zhou, X. 2011. A drought-induced pervasive increase in tree mortality across Canada's boreal forests. Nat. Clim. Change, **1**: 467–471. doi:10.1038/nclimate1293.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. Available from http://www.R-project.org/.

Robin, X., Turck, N., Haingard, A., Tiberti, N., Lisacek, F., Sanchez, J., and Müller, M. 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC Bioinf. **12**: 77. doi:10.1186/1471-2105-12-77.

Ryan, K.C., and Reinhardt, E.D. 1988. Predicting postfire mortality of seven western conifers. Can. J. For. Res. **18**(10): 1291–1297. doi:10.1139/x88-199.

Ryan, K.C., Knapp, E.E., and Varner, J.M. 2013. Prescribed fire in North American forests and woodlands: history, current practice, and challenges. Front. Ecol. Environ. **11**(Online Issue 1): e15–e24. doi: 10.1890/120329.

Salman, K.A., and Bongberg, W.J. 1942. Logging high-risk trees to control insects in the pine stands of northeastern California. J. For. **40**: 533–539.

Schwilk, D.W., Knapp, E.E., Ferrenberg, S.M., Keeley, J.E., and Caprio, A.C. 2006. Tree mortality from fire and bark beetles following early and late season prescribed fires in a Sierra Nevada mixed-conifer forest. For. Ecol. Manage. **232**: 36–45. doi:10.1016/j.foreco.2006.05.036.

Schwilk, D.W., Keeley, J.E., Knapp, E.E., McIver, J.D., Bailey, J.D., Fettig, C.J., Fiedler, C.E., Harrod, R.J., Moghaddas, J.J., Outcalt, K.W., Skinner, C.N., Stephens, S.L., Waldrop, T.A., Yaussy, D.A., and Youngblood, A. 2009. The national fire and fire surrogate study: effects of fuel reduction methods on forest vegetation structure and fuels. Ecol. Appl. **19**(2): 285–304. doi:10.1890/07-1747.1.

Sieg, C.H., Mcmillin, J.D., Fowler, J.F., Allen, K.K., Negron, F., Wadleigh, L.L., Anhold, J.A., and Gibson, K.E. 2006. Best predictors for postfire mortality of ponderosa pine trees in the intermountain west. For. Sci. **52**(6): 718–728.

Stephens, S.L., and Finney, M.A. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. For. Ecol. Manage. **162**: 261–271. doi:10.1016/S0378-1127(01)00521-7.

Stephens, S.L., Moghaddas, J.J., Edminster, C., Fiedler, C.E., Haase, S., Harrington, M., Keeley, J.E., Knapp, E.E., McIver, J.D., Metlen, K., Skinner, C.N., and Youngblood, A. 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecol. Appl. **19**(2): 305–320. doi:10.1890/07-1755.1.

Stephens, S.L., Agee, J.K., Fulé, P.Z., North, M.P., Romme, W.H., Swetnam, T.W., and Turner, M.G. 2013. Managing forests and fire in changing climates. Science, **342**: 41–42. doi:10.1126/science.1240294.

Stephenson, N.L. 1988. Climatic control of vegetation distribution: The role of the water-balance with examples from North America and Sequoia National Park, California. Ph.D. dissertation, Cornell University, Ithica, New York.

Thies, W.G., Westlind, D.J., Loewen, M., and Brenner, G. 2006. Prediction of delayed mortality of fire-damaged ponderosa pine following prescribed fires in eastern Oregon, U.S.A. Int. J. Wildland Fire, **15**: 19–29. doi:10.1071/WF05025.

Tomback, D.F., and Achuff, P. 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. For. Pathol. **40**: 186–225. doi:10.1111/j.1439-0329.2010.00655.x.

van Mantgem, P.J., Stephenson, N.L., Mutch, L.S., Johnson, V.G., Esperanza, A.M., and Parsons, D.J. 2003. Growth rate predicts mortality of *Abies concolor* in both burned and unburned stands. Can. J. For. Res. **33**(6): 1029–1038. doi:10.1139/x03-019.

van Mantgem, P.J., Stephenson, N.L., Keifer, M., and Keeley, J.E. 2004. Effects of an introduced pathogen and fire exclusion on the demography of sugar pine. Ecol. Appl. **14**(5): 1590–1602. doi:10.1890/03-5109.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H., and Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. Science, **323**: 521–524. doi:10.1126/science.1165000.

van Mantgem, P.J., Stephenson, N.L., Knapp, E., Battles, J., and Keeley, J.E. 2011. Long-term effects of prescribed fire on mixed conifer forest structure in the Sierra Nevada, California. For. Ecol. Manage. **261**: 989–994. doi:10.1016/j.foreco.2010.12.013.

van Mantgem, P.J., Nesmith, J.C.B., Keifer, M., Knapp, E.E., Flint, A., and Flint, L. 2013. Climatic stress increases forest fire severity across the western United States. Ecol. Lett. **16**: 1151–1156. doi:10.1111/ele.12151.

Waring, R.H. 1987. Characteristics of trees predisposed to die. BioScience, **37**(8): 569–574. doi:10.2307/1310667.

Westerling, A.L., Hidalgo, H.G., Cayan, D.R., and Swetnam, T.W. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. Science, **313**: 940–943. doi:10.1126/science.1128834.

Zarnoch, S.J., Bechtold, W.A., and Stolte, K.W. 2004. Using crown condition variables as indicators of forest health. Can. J. For. Res. **34**(5): 1057–1070. doi:10.1139/x03-277.

Ziegler, A., and Vens, M. 2010. Generalized estimating equations. Notes on the choice of the working correlation matrix. Methods Inf. Med. **49**: 421–432. doi:10.3414/ME10-01-0026.